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Protected areas buffer against harvest selection and rebuild phenotypic complexity

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Abstract. Harvest mortality typically truncates the harvested species' size structure, thereby reducing phenotypic complexity, which can lead to reduced population productivity, increased population variability, and selection on an array of life history traits that can further alter these demographic processes. Marine protected areas (MPAs) are a potential tool to protect older, larger individuals and therefore mitigate such ecological and evolutionary effects of harvest, depending on the degree of connectivity among areas. Such MPA protection relies on a shift in size-dependent mortality, the measurement of which can therefore serve as an early indicator of whether MPAs might achieve the desired longer-term ecological and evolutionary responses. We directly measured MPA effects on size-selective mortality and associated size structure using mark–recapture data on European lobster (*Homarus gammarus*) collected at three MPA–control area pairs in southern Norway during one decade (n = 5,943). Mark–recapture modeling, accounting for variation in recapture probabilities, revealed (1) that annual mean survival was higher inside MPAs (0.592) vs. control areas (0.298) and (2) that significant negative relationships between survival and body size occurred at the control areas but not in the MPAs, where the effect of body size was predominantly positive. Additionally, we found (3) that mean and maximum body size increased over time inside MPAs but not in control areas. Overall, our results suggest that MPAs can rebuild phenotypic complexity (i.e., size structure) and provide protection from harvest selection.

Key words: capture–recapture; fisheries-induced selection; lobster; marine protected areas; size structure; Skagerrak; survival; vital rates.

Introduction

Individual vital rates determine the overall population productivity of harvested marine species, with older, larger individuals typically having disproportionately greater reproductive output than smaller and younger conspecifics (Birkeland and Dayton 2005, Barneche et al. 2018). In addition to determining overall productivity, size-dependent mortality determines expectations for population-level response to environmental variability in harvested species: if individuals live to older ages, with associated larger sizes, then the higher survival buffers the total population size against environmental variability and years of poor reproductive output (Planque et al. 2010). Stated simply, fisheries cause a change in size-dependent mortality within harvested populations (Shin et al. 2005). Changes in size-dependent mortality in harvested populations can reduce overall productivity and increase the harvested population's sensitivity to environmental variability (Planque et al. 2010), which then alters the stability of population dynamics and harvestable yields (Anderson et al. 2008, Schindler et al. 2010). A shift in size-dependent mortality with fisheries can also shift selection on an array of life history traits (e.g., toward smaller body size, earlier maturity, and

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greater reproductive investment at earlier stages) that determine size-dependent vital rates, such that any resulting fisheries-induced evolution will further alter population productivity and variability (Hutchings and Fraser 2008). If such shifts are adaptive, then a typical expectation is that they will increase the overall population growth rate compared to no adaptation for a given, ongoing level of intensive fishing. However, fishing regimes that drive such evolutionary change can lead to population viability and biomass yield with lower robustness to uncertainty, stochasticity, and disturbances than management approaches that reduce fisheries-induced evolution (Ratner and Lande 2001, Baskett et al. 2005, Audzijonyte and Kuparinen 2016 [but note an exception to this expectation in a model where growth is density dependent and growth speed trades off with body size; Kuparinen and Hutchings 2012]).

One management tool to protect older, larger, and more fecund individuals in harvested populations is to establish marine protected areas (MPAs), i.e., areas with partially or fully restricted harvest. Marine protected areas often have an array of goals in terms of biodiversity conservation and fisheries sustainability (Leslie 2005). For example, due to a release from fishing mortality, the initial expected (White et al. 2013) and observed (e.g., Taylor and McIlwain 2010) response to MPAs is a "filling in" of the age and size structure of harvested populations through a reduction in mortality, thereby allowing individuals to survive to older ages and larger sizes. This response is the underlying driver of expected ecological and evolutionary consequences of MPAs. Specifically, from an ecological perspective, MPAs are expected to increase population size and biomass (frequently observed for harvested species; Claudet et al. 2008, Lester et al. 2009), and subsequently increase productivity and reduce population variability (reviewed by Baskett and Barnett 2015). From an evolutionary perspective, MPAs are expected to provide protection against harvest selection (Baskett et al. 2005, Villegas-Ríos et al. 2017). Note that the potential for these effects to manifest depends on larval dispersal and post-larval settlement movement rates, which vary substantially across harvested species. In general, species with greater post-larval movement rates experience lower capacity for MPA protection and therefore demographic responses (Walters et al. 2007, Moffitt et al. 2009), and species with greater larval dispersal can experience lower potential for protection against fisheries-induced evolution (Baskett et al. 2005). However, when movement is constrained enough relative to MPA size, MPAs can reduce population variability, but demonstrating this effect of MPAs requires long-term time series (e.g., Babcock et al. 2010). Similarly, characterizing evolutionary responses to MPAs requires long-time series, in part because evolutionary responses to MPAs might entail long time lags (Hutchings and Fraser 2008). Even responses expected to occur rapidly, such as increases in population size and biomass, might be difficult to detect if recruitment is highly stochastic (e.g., Starr et al. 2015).

MPAs can only increase productivity, decrease variability, and protect against fisheries-induced evolution if they differ in the underlying driver of these dynamics, i.e., size-dependent mortality, compared to both before MPA establishment and harvested areas. Therefore, a difference in size-dependent mortality through time and space can serve as an early indicator of MPA efficacy in achieving the desired longer-term ecological and evolutionary outcomes. Furthermore, quantification of natural (inside-MPA) size-dependent mortality is essential to developing expectations for demographic responses to MPAs and therefore informing an adaptive management process of evaluating whether MPAs are working as expected, and if not, what adjustments to knowledge or management are necessary (White et al. 2011, 2013). A direct method of estimating vital rates is by analyzing individual mark-recapture data collected before and after MPA implementation, but because of the long-term monitoring and protection requirements of the target populations, such data sets and knowledge are rare (Miethe et al. 2010; but see Moland et al. 2013).

In 2006, several MPAs were established along the Skagerrak coast in southeastern Norway to protect the European lobster (*Homarus gammarus*) from overharvesting. Within these MPAs, only hook and line type fishing is allowed and the fixed fishing gear types used to harvest lobster are banned. Therefore, all MPAs are no-take lobster MPAs, but they also offer partial protection to other species within their boundaries, such as the Atlantic cod (*Gadus morhua*), which can only be harvested using hook and line gears. The expected benefits inside these MPAs soon became detectable. For instance, catch-per-unit-effort (measured through scientific surveys) and mean size of both European lobsters and Atlantic cod increased in MPAs compared to control sites (Moland et al. 2013). Additionally, in the case of cod, it was reported from one of the more intensively studied sites that fishing mortality decreased, and survival doubled after the MPA was established, remaining high in the MPA relative to harvested control areas (Fernández-Chacón et al. 2015). The ongoing monitoring of these MPAs and nearby harvested sites provides a unique opportunity to explore how size-dependent mortality has shifted through time following MPA establishment, and the demographic and evolutionary consequences of any changes to size structure.

Here we provide a first direct empirical assessment of MPA effects on the strength, direction, and form of size-dependent mortality using data from European lobster in three MPA-control area pairs distributed along the Norwegian Skagerrak coast. We examine the temporal patterns of size-specific survivorship and explored trends in size structure at these same sites, thereby allowing us to connect changes in vital rates (survivorship) to demographic change (size distribution). We hypothesized that differences in vital rates would lead to larger lobsters

inside MPAs compared to harvested sites. Consequently, we expected survival of large individuals to increase and the size distribution to broaden in protected versus harvested sites with time since MPA establishment. In addition to the potential for longer-term ecological responses in terms of population productivity and stability, our analyses test the capacity for MPAs to protect against harvest selection and therefore eventual evolutionary responses.

Methods

Study system

Located on the Norwegian Skagerrak coast, the MPAs included in this study were established to generate knowledge on the development of lobster populations in areas unaffected by extractive fishing (Pettersen et al. 2009). The three MPA sites studied, listed from west to east in Skagerrak, are (1) Flødevigen, in Aust-Agder County (58°25′ N, 8°45′ E), (2) Haneflu, in Vestfold County (59°13′ N, 10°31′ E), and (3) the small island Kvernskjær (59°02′ N, 10°58′ E) in Østfold County (Fig. 1). Control areas open to lobster fishing are located adjacent to these and separated from MPAs by distances of 1,700 m, 850 m, and 2,250 m (from MPA center to control area center) in Aust-Agder (Gjervoldsøy), Vestfold (Bolærne), and Østfold (Vikertangflu), respectively (Fig. 1). At each location, the MPAs and control areas are of approximately equal size (~1, 0.7, and 0.5 km^2 in Aust-Agder, Vestfold, and Østfold, respectively). All capture of lobster has been effectively banned in the MPAs since September 2006 through gear restrictions, with only hook and line fishing allowed (Moland et al. 2013). Policing of the MPAs is based on collaboration between the Directorate of Fisheries, the Coast Guard, and local police.

Study species

The European lobster is a large decapod crustacean of ecological and commercial importance, distributed from the north of Norway to Morocco in North Africa (Triantafyllidis et al. 2005), with a life expectancy of several decades (Sheehy et al. 1999). In Norway, European lobster reaches sexual maturity at ~23 cm total length (TL, measured from the tip of the rostrum to the end of the middle uropod), with a near linear increase in fecundity with body size (Agnalt 2008). The species is considered a nocturnal animal, where light hours are generally spent solitary inside shelters on rocky bottoms (Smith et al. 1999, Mehrtens et al. 2005, Moland et al. 2011*b*). European lobsters rarely move more than a few kilometers for periods up to years (Dannevig 1936, Smith et al. 2001, Agnalt et al. 2007, Thorbjørnsen et al. 2018). Recent shorter-term home-range studies based on acoustic tracking yielded estimates ranging from 0.01 to 0.64 km^2 over periods ranging from several months to nearly 1 yr (Moland et al. 2011*a*, Wiig et al. 2014, Skerritt et al. 2015). In Norway, fishery catch-per-unit-effort has decreased by 65% from the 1950s to 2000s (Pettersen et al. 2009). As of 2008, lobsters in Norway are legally caught in traps fitted with two circular escape vents measuring 60 mm in diameter during a 2-month season (1 October to 30 November). In the same year, minimum legal size was increased from 24 to 25 cm TL, along with a trade and landings ban on egg-bearing females. As of 2017, a maximum legal size of 32 cm TL was introduced in southern Norway. Effort (total number of gear deployed) is limited to 10 and 100 traps per recreational and commercial participants, respectively. Total effort remains unknown in the fishery, which is dominated by recreational participants, but trap density has been estimated as high as ~50 traps/km^2 during the first week of the season (Kleiven et al. 2011). Over the 2-month fishing season, harvest mortality may be as high as 75% (Moland et al. 2019). A network of marine protected areas in Skagerrak (the same as studied herein) has demonstrated the usefulness of MPAs in rebuilding local lobster populations (Moland et al. 2013).

Sampling design

An annual standardized research trapping survey, including capture–mark–recapture, was conducted inside the proposed MPA areas during three consecutive years prior to MPA designation (2004–2006). In 2006, in the last sampling season prior to implementation of the MPAs, adjacent control areas approximately matching MPA size and habitat structure were designated and included in the survey (2006–2015). Such control areas were needed so the dynamics of lobster populations under opposite levels of harvest pressure (but in otherwise similar coastal habitats) could be compared over time. MPA habitats were assessed by SCUBA surveys, and include rock and boulder fields with macroalgae, as well as sand and mud flats (Pettersen et al. 2009). Lobsters were sampled using standard "parlor" traps (900 × 450 × 400 mm with 120 mm entrances) baited with frozen mackerel (*Scomber scombrus*). Single traps were deployed at 10–30 m depth throughout the areas sampled. The standardized annual sampling effort (100 traps per day) was spread over four days using 50 traps in each region (25 traps simultaneously in MPA and control area) in each year, with approximately 24 h soak time. Sampling was conducted between 20 August and 10 September in each year, during the same week in each region, and simultaneously inside MPAs and control areas after 2006.

Lobsters were measured and tagged immediately upon capture and released at the site of capture. Total length (TL) was measured to the nearest mm from the tip of the rostrum to the posterior margin of the telson. Sex was determined by examination of the first pair of pleopods. All lobsters caught were tagged with individually numbered T-bar anchor tags (TBA2, 45 × 2 mm,

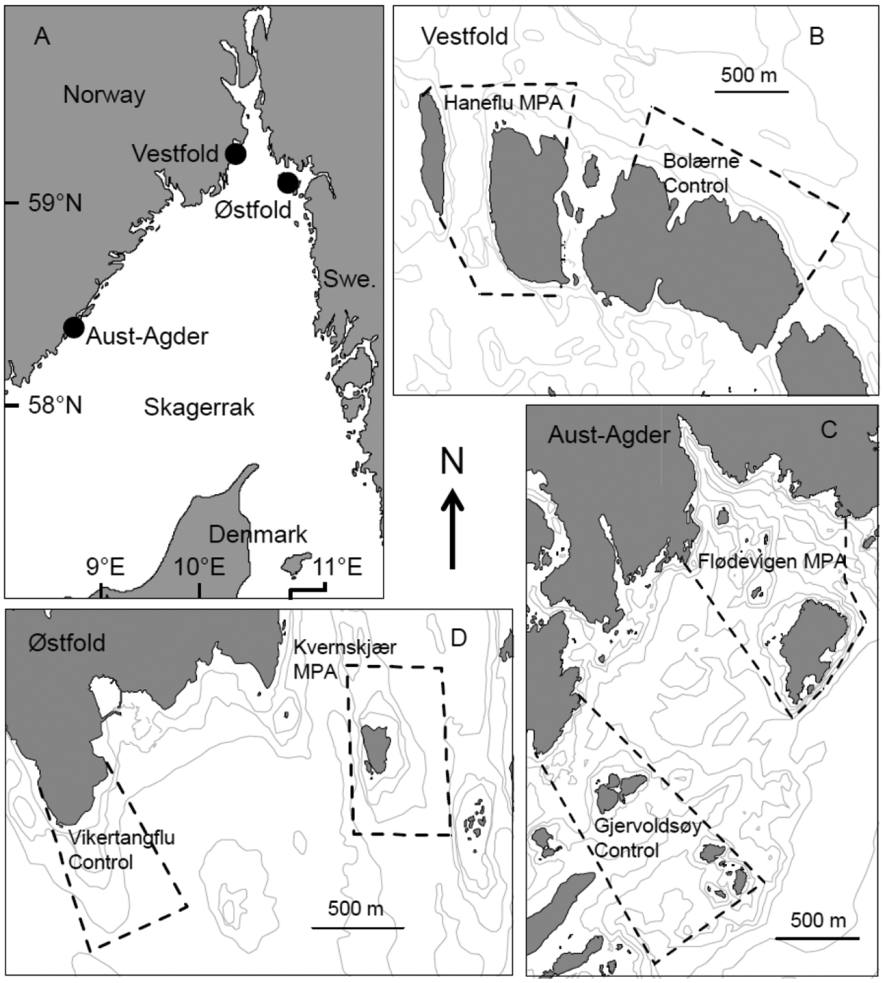

FIG. 1. Clockwise from top: (A) dark circles show the location of marine protected areas (MPA) and control area pairs in Skagerrak, (B) the Haneflu MPA and Bolærne control area in Vestfold county, (C) the Flødevigen MPA and Gjervoldsøy control area in Aust-Agder, and (D) the Kvernskjær MPA and Vikertangflu control area in Østfold.

Hallprint Pty., Holden Hill, South Australia, Australia) with printed information about the ongoing project. Tags were inserted in the ventral musculature between the cephalothorax and abdomen, to the right side of the midline using a standard tag applicator. Placing the tag in this area ensures its retention through multiple molts (Agnalt et al. 2007).

Mark–recapture data analysis and modeling of survival

Mark–recapture data collected at the study sites were summarized in individual encounter histories made of sequences of binary encounters indicating, for each tagged individual, whether it was found (1) or not (0) at each sampling occasion. Each annual sampling season was defined as an encounter occasion and only one observation per year (detection or non-detection) was retained. To investigate spatiotemporal changes in survival–length relationships, encounter history data were segmented in four periods; a before-protection period (2004–2006) and three post-protection periods: early (2006–2009), intermediate (2009–2012), and late (2012–2015). Such splitting was necessary to account for temporal variation in body length in our subsequent capture–recapture analyses, and at the same time allowed us to both compare parameter estimates under different modes management (before vs. after protection) and track changes in survival responses with increasing MPA age (i.e., over regular time intervals after protection). The number of encounter occasions included within each period (three or four occasions) was enough to obtain separate survival and recapture probability estimates (Lebreton et al. 1992), and the specific annual intervals over which survival probability was estimated did not overlap among periods (i.e., they were not analyzed twice).

Due to fewer years of sampling before MPA implementation, fewer occasions were included in the pre-

protection period compared to the post-protection periods. Because only the planned MPA sites were sampled before 2006, encounter data from pre-protection years were unified in a single data set that included the three planned MPAs in Aust-Agder, Vestfold, and Østfold, leading to a final number of 10 independent sets of encounter data (period and region combinations) for statistical analysis. In our models, site (MPA or control area) was treated as a categorical (group) variable and total length (cm) as an individual covariate. For the unique pre-protection period, group categories referred only to the study MPAs (three groups), as no control areas were sampled then, whereas for the region-specific post-protection periods, group categories reflected the local MPA and control area sites within each region (two groups). We used individual length measures obtained at the first encounter within the corresponding time period in order to relate them to survival and/or recapture rates over the entire period. With this approach, we assumed the influence of body length on the estimated parameters to be the same over the next two to three annual intervals, but not longer. Different sets of length values, reflecting the range of body sizes seen at each location within each time window, were used in each region- and period-specific analysis, thus accounting for potential changes in body size between periods. Length covariates were standardized before the analyses to mean = 0 and standard deviation = 1 by using the formula: $z = x - \mu/\sigma$, where z is the standardized length value, x is the original length value, and μ and σ are the sample mean and standard deviation, respectively. This rescaling of the covariate helped the numerical optimization algorithm to find the correct parameter estimates during the modeling process.

Survival analyses were performed in program MARK (White and Burnham 1999) and estimates were obtained by applying classical Cormack-Jolly-Seber models (CJS) to the data. CJS models allow estimation of both apparent survival (Φ) and recapture probabilities (p), and also testing of group or covariate effects on these parameters (Lebreton et al. 1992). However, this approach does not allow for time variation in individual covariates, so our encounter data had to be segmented in different time periods and analysed using updated individual covariate values for each time window to overcome this limitation. In addition, CJS models can only estimate apparent survival, as emigration from the study area is confused with true mortality; however, given the sedentary behavior of adult lobsters (Moland et al. 2011*a*), permanent emigration is likely to be low in our system, so the obtained apparent survival rates might be close to true survival. Prior to the analyses in MARK, we performed a goodness-of-fit (GOF) test to ensure that the assumptions of CJS models were met by the data (identity of rates and independence of fates among individuals; Lebreton et al. 1992). GOF testing was performed using U-CARE (Choquet et al. 2009), a statistical program with contingency tables that inform users about different aspects of the data and help to identify sources of heterogeneity that violate model assumptions. Eventually, overdispersion coefficients ($\hat{c}$) are calculated from the global results of each GOF test and applied, if necessary, to the subsequent analyses to correct for lack of fit.

We conducted 10 independent survival analyses in MARK (one for the pre-protection period and nine for the post-protection periods) and several CJS models were built, departing from a general model with group (site) effects on Φ and p. We started removing group effects from the p parameter to simplify the model structure, and to test whether p was identical (or not) between sites. Then, we kept the best of the two former models and tested for linear and quadratic effects of length on p until a final structure was retained for this parameter. Then, we focused on the survival parameter, modeling length effects in a departure model with only group effects on Φ. In the pre-protection analysis, this was done by building 21 models combining constancy (.), linear (L) and quadratic (L^2) effects of length on Φ at each MPA separately ($\Phi_{\text{Aust-Agder}}$, Φ_{Vestfold}, $\Phi_{\text{Østfold}}$) plus three additional models with a single survival parameter and no group effects. In the post-protection analyses, we always kept group effects on Φ and built nine models combining constancy and length effects on Φ within the MPA (Φ_{res}) and the control area (Φ_{con}) separately. Year effects on survival and/or recapture probabilities and within-period variation in length-survival relationships were not examined to avoid unnecessary increases in model parameters and estimation problems associated with further data segmentation, respectively. Model selection was based on the Akaike Information Criterion corrected for overdispersion (QAIC). The model scoring the lowest QAIC value of the set was considered best supported (i.e., most parsimonious one) and those differing in less than two points of QAIC from the best model (ΔQAIC < 2) were treated as statistically equivalent. In the case of several models receiving similar statistical support, we used model averaging to obtain reliable survival estimates. To examine the relationship between apparent survival and length at each site and time period, we used beta slope estimates extracted from the highest ranked models containing individual covariate effects on Φ.

Size complexity analysis

We calculated three indicators of population size complexity to explore changes in size structure through time: mean body size, standard deviation of body size, and 90th percentile of body size. The 90th percentile was used as a proxy of the abundance of large individuals that are predicted to result from the filling in age structure of the population. The 90th percentile and standard deviation of body size were first estimated for each combination of year and area. We first investigated the overall effect of protection on those three indicators by running linear mixed-effects models (one per indicator)

with year (scaled to mean of 0 and SD of 1), treatment (MPA vs. control area) and their interaction as fixed effects, and region as a random effect. In these models, we were interested in differences in the interaction term year × treatment that would indicate a different response of size complexity indicators over time between MPA and control areas. We then conducted a more detailed analysis of the variation in the three size complexity indicators over time to inspect differences between each MPA–control-area pair. For this, we used linear models (one per indicator) with year (scaled to mean of 0 and SD of 1), area (categorical variable with six levels), and their interaction as explanatory variables. In these models, we were specifically interested in the interaction year × area as an indicator of differences in how population structure changed in the different locations. All models were fit using the nlme library in R (Pinheiro et al. 2017). We used a backward model simplification approach, starting with a maximal model that included all fixed effects and sequentially removing the least significant term from the model (the threshold P value was set at 0.05). We tested the significance of the slope at each location (i.e., trend over time) obtained from the optimal linear models using the testInteractions function in the phia package in R (De Rosario-Martinez 2013) whenever the interaction area × year was significant. We used the same function to test differences in slopes between each MPA–control pair.

Results

A total of 6,186 lobsters were tagged during the study, with 1,445 individuals being recaptured at least once and 104 seen four or more times. More lobsters were sampled inside (n = 3,633) vs. outside MPAs (n = 2,553), and more recaptures were obtained within protected areas (n = 826) compared to harvested (control) areas (n = 619). Frequency of recaptures decreased with time since tagging, but individuals were still re-encountered even 7 yr after the first observation (see Appendix S1). Total length of newly tagged lobsters ranged from 15.4 cm to 40.8 cm (mean = 24.6 cm) whereas recaptured individuals ranged in length from 16.8 cm to 42.2 cm (mean = 27.5 cm). Observed mean body growth ranged between 2.4 and 3.4 cm within the study periods considered here. For extended time periods (i.e., 2004–2015), difference in body length between first and last observation could be as high as 17 cm.

Mark–recapture model selection and parameter estimates

Results of the global GOF tests performed for each capture–recapture data set typically yielded $\hat{c}$ values around 1, indicating good fit of CJS models to the data (see Appendix S2). Estimated recapture probabilities (mean ± SE) ranged between 0.292 ± 0.101 and 0.685 ± 0.144 and were influenced by total length at all sites, but only during the post-protection period (Appendix S3). During the post-protection period, both linear and quadratic effects of length were retained, without a clear spatiotemporal pattern, and generally pointed to a lower detectability of large-sized individuals (Appendix S4).

Constancy (i.e., no length effect) and identical survival among MPAs was the most parsimonious model structure in the analysis of pre-protection data (Model 1; Table 1), but body length effects on survival were also well supported, as the inclusion of the length covariate in the top ranked model yielded statistically equivalent results (Model 2; Table 1). During the analysis of post-protection data, models containing length effects on survival were commonly selected and highly ranked (Table 2). The most common top ranked model of lobster survival after MPA implementation included body length effects on survival at the harvested areas, but not at the MPAs (Table 2). This model was selected in all regions and post-protection time periods, with the exception of the late period at Vestfold- and Østfold regions, when length effects were top ranked at the MPAs but not at harvested areas (Table 2). Model-averaged estimates extracted from constant survival models (i.e., excluding length effects on survival) indicated that apparent survival (Φ) peaked at all MPAs immediately after protection and then declined, but later values remained elevated compared to those from the corresponding control areas and pre-protection years (Fig. 2). Mean Φ after protection (2006–2015) was two times higher at the MPAs (geometric mean of constant survival estimates from reserves; n = 9; Φ_{res} = 0.582) compared to the control areas (geometric mean of constant survival estimates from control areas; n = 9; Φ_{con} = 0.298).

When focusing on the subset of models with length effects on either Φ_{res} or Φ_{con}, results showed differences between MPA and control areas in the form and sign of the best length–survival relationships: both linear and quadratic effects were amongst the higher ranked models for the MPAs, with linear effects being better supported (i.e., scoring lower QAIC) than quadratic ones most of the time (Table 2, Fig. 3). At the MPAs, the sign of the linear relationship was negative before protection (β estimate ± SE = −0.070 ± 0.064; extracted from model 2, Table 1) and more often positive than negative after protection (six out of nine linear coefficients were positive; Fig. 4). At the control areas, linear effects of length on Φ were usually top ranked (Table 3), with a higher frequency of negative slopes (six out of nine linear coefficients were negative; Figs. 3 and 4).

Size complexity

Overall we found that mean body length was larger and increased at a higher rate inside MPAs as compared to control areas (Appendix S5: Table S1, Fig. S1a). In particular, mean body length significantly increased in all the marine MPAs over the period 2004–2015 at an average rate of 11.6 mm/yr. Results for the control area

TABLE 1. Model selection results showing the different models structures tested on apparent survival parameters (Φ) during the analysis of data from the pre-protection period (2004–2006).

Model	$\Phi_{(\text{Aust-Agder})}$	$\Phi_{(\text{Vestfold})}$	$\Phi_{(\text{Østfold})}$	QAIC_c	ΔQAIC_c	Np
1	**(.)**	**(.)**	**(.)**	***209.4747***	**0**	**2**
2	(*L*)	(*L*)	(*L*)	*211.3965*	1.9218	3
3	(.)	(.)	(.)	213.3162	3.8415	4
4	(L^2)	(L^2)	(L^2)	213.318	3.8433	4
5	*L*	(.)	(.)	213.9028	4.4281	5
6	(.)	(.)	*L*	214.9225	5.4478	5
7	(.)	*L*	(.)	215.0181	5.5434	5
8	*L*	(.)	*L*	215.5301	6.0554	6
9	*L*	*L*	(.)	215.6194	6.1447	6
10	L^2	(.)	(.)	215.6259	6.1512	6
11	(.)	*L*	*L*	216.6426	7.1679	6
12	(.)	(.)	L^2	217.0153	7.5406	6
13	(.)	L^2	(.)	217.1128	7.6381	6
14	*L*	*L*	*L*	217.2652	7.7905	7
15	L^2	*L*	*L*	219.0222	9.5475	8
16	*L*	*L*	L^2	219.3914	9.9167	8
17	*L*	L^2	*L*	219.3933	9.9186	8
18	L^2	(.)	L^2	219.3967	9.922	8
19	L^2	L^2	(.)	219.487	10.0123	8
20	(.)	L^2	L^2	220.88	11.4053	8
21	L^2	*L*	L^2	221.1653	11.6906	9
22	L^2	L^2	*L*	221.1672	11.6925	9
23	*L*	L^2	L^2	221.5364	12.0617	9
24	L^2	L^2	L^2	223.3275	13.8528	10

Notes: Model notation: *L*, linear effect of body size on survival probability; L^2, quadratic effect of body size on survival probability; (.), constant survival probability (see also *Methods*). QAIC_c (where QAIC_c is the Akaike Information Criterion corrected for overdispersion and sample size) values of high-ranked ($\Delta\text{QAIC}_c < 2$) models are italicized, whereas the most parsimonious (lowest QAIC_c) one is shown in boldface type. Np, number of parameters.

TABLE 2. Model selection results showing the nine structures tested on survival and the QAIC values obtained in the analysis of each regional subset of data from the post-protection period (T1, 2006–2009; T2, 2009–2012; T3, 2012–2015).

Model		QAIC								
Φ_{res}	Φ_{con}	Aust-Agder T1	Aust-Agder T2	Aust-Agder T3	Vestfold T1	Vestfold T2	Vestfold T3	Østfold T1	Østfold T2	Østfold T3
L	*L*	219.860†	436.290	472.586	553.547†	1204.521	710.291	940.395†	1005.340	1477.217†
L	L^2	221.924	436.566	473.941	555.562	1205.614	712.142	942.033	1005.100†	1479.245
L^2	*L*	221.276	438.242	473.949	552.976†	1205.439	709.880†	940.252†	1007.011	1477.796†
L^2	L^2	223.285	438.521	474.619	555.001	1205.466	711.643	941.880	1006.660	1479.765
(.)	(.)	224.966	434.707†	471.574†	551.842†	1208.055	710.270	940.632†	1011.743	1484.490
(.)	*L*	**218.332†**	**434.270†**	**470.113†**	**551.572†**	**1202.495†**	711.904	**939.396†**	**1003.335†**	1485.938
(.)	L^2	220.390	434.538†	474.218	553.580	1203.584†	713.758	941.024†	1003.399†	1485.572
L	(.)	226.469	436.717	473.2570	553.810	1209.139	709.235	939.578†	1011.792	**1476.298†**
L^2	(.)	227.7776	438.6573	472.415	553.2155†	1210.9554	**708.1549†**	941.0898	1013.7637	1477.8066†

Notes: Model notation: Φ_{res}, survival probability within marine protected areas (MPA); Φ_{con}, survival probability within control area; *L*, linear effect of body size on survival probability; L^2, quadratic effect of body size on survival probability; (.), constant survival probability (see also *Methods*). The dagger symbol (†) denotes high-ranked ($\Delta\text{QAIC} < 2$) survival models, whereas the most parsimonious (lowest QAIC) ones are shown in boldface type.

revealed a smaller but significant increase, 5.5 mm/yr on average, in Bolærne and Vikertangflu, and no significant trend over time in Gjervoldsøy for the period 2006–2015 (Table 3). Accordingly, we found that all marine MPAs resulted in higher increases of body length than their neighboring control areas (the increase was 7.5 mm/yr higher on average inside the marine MPAs; Table 4, Figs. 5 and 6).

We found that the standard deviation of body length was larger inside MPAs, and we found a significant

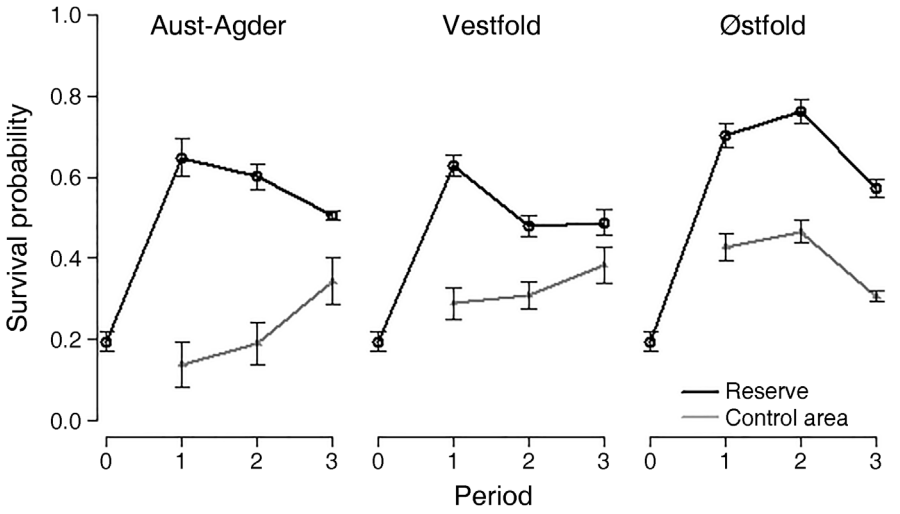

FIG. 2. Constant apparent survival estimates (Φ) of lobster obtained for each region, site (MPA, black line; control area, grey line) and time period (0, pre-protection period; 1–3, early, intermediate, and late post-protection periods, respectively). Point estimates and SE (bars) were model-averaged from the outputs of high ranked models (ΔQAIC < 2, where QAIC is the difference in Akaike Information Criterion corrected for overdispersion) obtained in each analysis.

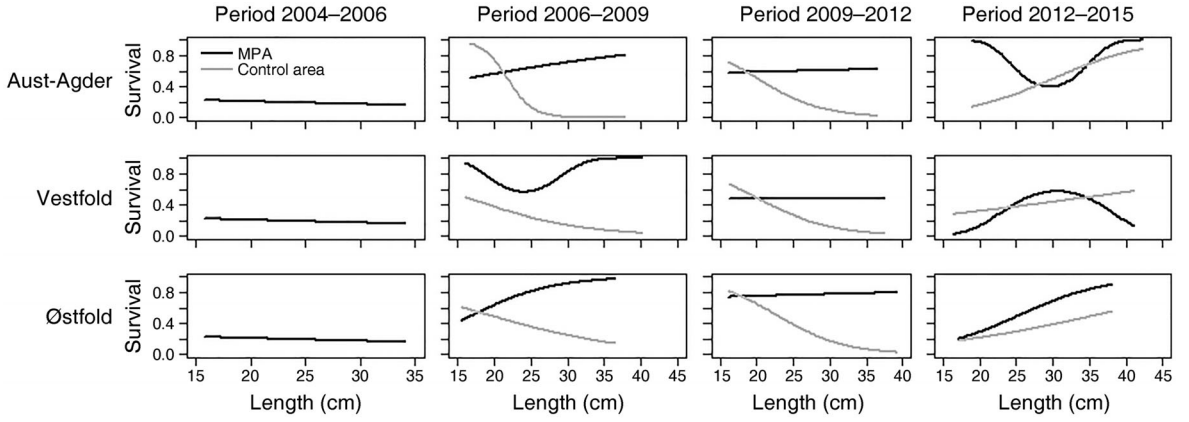

FIG. 3. Predicted survival with length for each region, area (MPA, control) and time period. Predicted values for each study area come from the highest ranked (i.e., lowest AIC) structure with length effects (linear or quadratic) on survival at that site. Note that such structures do not always coincide with the most parsimonious ones in the full set of models (see *Results*).

increase over time of this indicator inside MPAs but no trend over time inside control areas (Appendix S5: Table S1, Fig. S1b). In particular, we observed that all marine MPAs showed an increase in standard deviation over the period 2004–2015, although this increase was only significant in Flødevigen (4.65 mm/yr). Conversely, the opposite pattern was observed in the control areas where the standard deviation of length tended to decrease from 2006 to 2015, but the trends were not significant (Table 3). Accordingly, when comparing pairs of treatments, all MPAs tended to have a higher net increase of standard deviation as compared to their neighboring control areas, but this difference in net increase was only significant between one MPA-control pair (Flødevigen and Gjervoldsøy, respectively; 4.52 mm/yr) (Table 4).

Our results indicate that the 90th percentile of body length was larger inside MPAs than in control areas, and that in both cases, this indicator increased over time although at a significantly higher rate inside MPAs (Appendix S5: Table S1, Fig. S1c). Specifically, the 90th percentile of body length increased at all MPAs from 2004 to 2015 at an average rate of 17.4 mm/yr. In the control areas, however, the model revealed a significant increase in Bolærne (10.73 mm/yr), but highly nonsignificant results in Gjervoldsøy and Vikertangflu (Table 4). This resulted in a significantly higher increase of the 90th percentile in Flødevigen (MPA) as compared to Gjervoldsøy (control) and in Kvernskjær (MPA) as compared to Vikertangflu (control) (15.0 mm/yr higher in the marine MPAs on average), but no differences between the Haneflu- and Bolærne MPA–control pairs (Table 4).

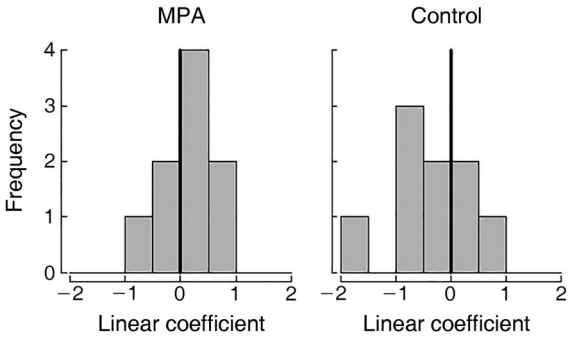

FIG. 4. Histograms showing the frequencies obtained at the MPAs (left) and control areas (right) for different values of the linear (β) coefficients describing the relationship between individual survival and length during the post-protection period. For each combination of site and time period, β estimates were extracted from the lowest QAIC structure within the subset of models with linear length effects on survival (see *Results*).

DISCUSSION

By combining the analysis of body length data of European lobster with the analysis of a unique data set with thousands of individual encounters collected during a 12-yr mark–recapture study at replicated protected and harvested sites, we simultaneously examined changes in length-specific survival and size structure over time. Overall, we found that lobster survival and size complexity increased within protected areas whereas survival was lower and lobsters typically smaller in areas open to harvesting. We documented that MPAs can provide protection from harvest selection, with immediate consequences for size structure and expected longer-term consequences for population productivity and variability.

Apparent survival of European lobster remained at low levels in areas open to harvesting but peaked after protection via MPA establishment and remained higher in the MPAs compared to control areas, a pattern consistent with the absence of harvest and evidence that local protection has benefits for lobster vital rates. Lower survival of lobster in control areas seemed to be driven by the higher mortality of large-sized individuals, as negative effects of total length on individual survival often received the highest statistical support. Protection from harvest, on the other hand, increased apparent survival rates of lobster in all MPAs, and in some of them (e.g., Flødevigen, in Aust-Agder County) there was statistical support for a shift from negative to positive linear effects of length on survival immediately after protection. Previous studies conducted in Aust-Agder and Østfold regions (Moland et al. 2011*a*, Huserbråten et al. 2013) have also revealed high annual survival of acoustically tagged lobsters inside MPAs over a 12-month period, and multiyear studies conducted within the same MPA network have reported temporal

TABLE 3. Temporal trends in the selected size-structure indicators (mean, standard deviation, and 90th percentile of individual size) of European lobster at each MPA and control area.

	Mean size				Standard deviation				90%			
Area	*N*	Intercept	Slope	*P*	*N*	Intercept	Slope	*P*	*N*	Intercept	Slope	*P*
MPA												
Flødevigen	1096	274.5	12.4	<0.001	12	35.36	4.65	<0.001	12	315.048	21.18	<0.001
Haneflu	2277	263.6	10.1	<0.001	12	33.36	1.43	0.12	12	302.47	15.80	<0.001
Kvernskjær	2284	251.3	12.2	<0.001	12	33.22	0.33	0.71	12	300.23	15.20	<0.001
Control												
Gjervoldsøy	496	194.3	1.4	0.329	10	27.68	0.13	0.91	10	280.84	1.03	0.70
Bolærne	1149	218.6	7.1	<0.001	10	30.69	−0.39	0.74	10	277.22	10.73	<0.001
Vikertangflu	2032	163.3	3.9	<0.001	10	26.59	−1.28	0.29	10	273.05	2.31	0.40

TABLE 4. Differences between each MPA–control pair in the selected size-structure indicators (mean, standard deviation, and 90th percentile of individual size) of European lobster.

	Differences in mean size				Differences in standard deviation				Differences in 90%			
Area	Intercept	*P*	Slope	*P*	Intercept	*P*	Slope	*P*	Intercept	*P*	Slope	*P*
Flødevigen-Gjervoldsøy	24.312	<0.001	11.047	<0.001	7.678	<0.001	4.516	<0.001	34.211	<0.001	20.141	<0.001
Haneflu-Bolærne	21.776	<0.001	2.997	0.014	2.688	0.068	1.820	0.227	25.249	<0.001	5.075	0.143
Kvernskjær-Vikertangflu	18.675	<0.001	8.335	<0.001	6.631	<0.001	1.608	0.285	27.188	<0.001	12.894	<0.001

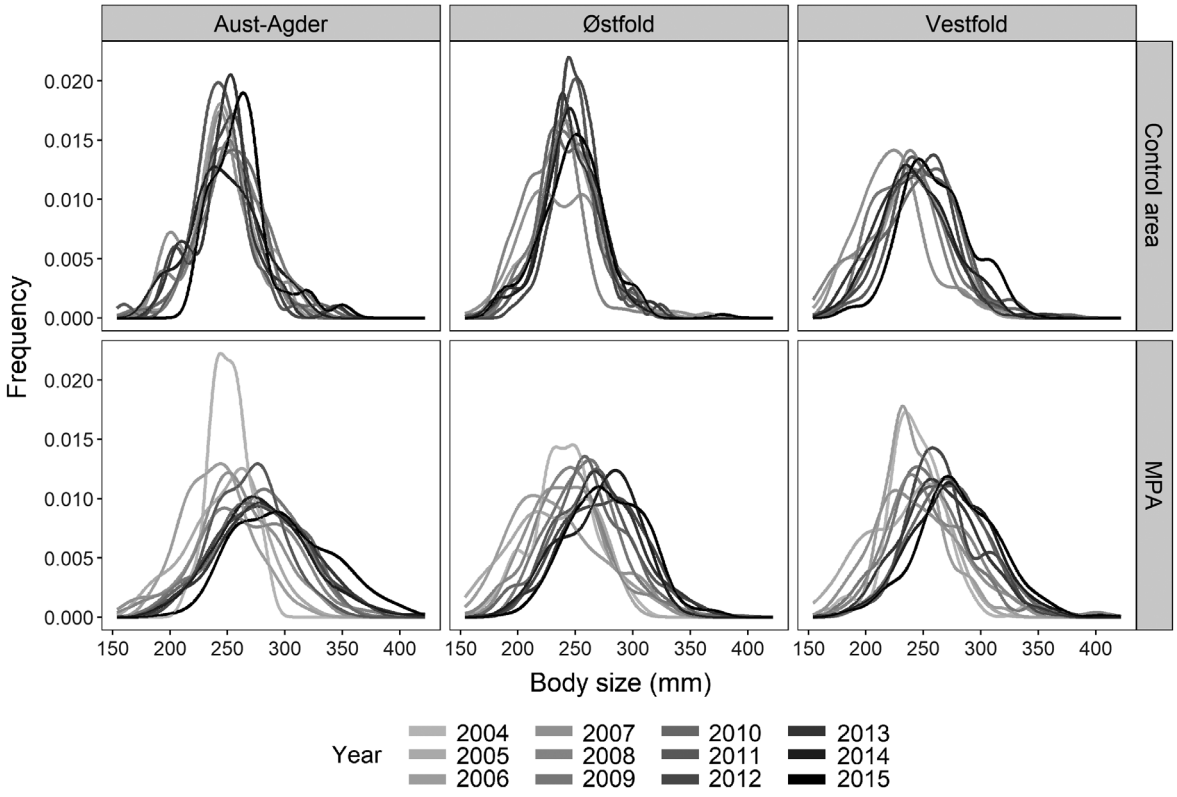

FIG. 5. Size distribution of European lobsters inside three MPAs and three control areas in southern Norway for the period 2004–2015.

increases in catch-per-unit-effort (a proxy of abundance), consistent with the survival benefits reported here (Huserbråten et al. 2013, Moland et al. 2013).

The increased survival of lobster, including large individuals, inside MPAs was reflected in a rapid change in the size structure characterized by an increase of the large-sized fraction of the population with a subsequent increase in mean size. The diversity of sizes inside protected areas tended to increase, although results were not always significant. The rapid demographic changes inside MPAs favoring larger individuals are expected to have immediate ecological effects. First, increased reproductive output is expected from the abundance of larger females inside the MPAs (Barneche et al. 2018). Indeed, both mean egg size and pelagic larval survival of European lobster increase with maternal size meaning that such large females may disproportionately contribute to offspring production in the population (Moland et al. 2010). Second, a more filled-in size structure could lead to decreased variability in response to perturbations (Planque et al. 2010) enhancing the long-term benefits of MPAs. Recently, Roberts et al. (2017) reviewed the ways in which marine protection by means of marine reserves and MPAs can mitigate and promote adaptation to climate change. They explored how such managed ecosystems can buffer against uncertainty in

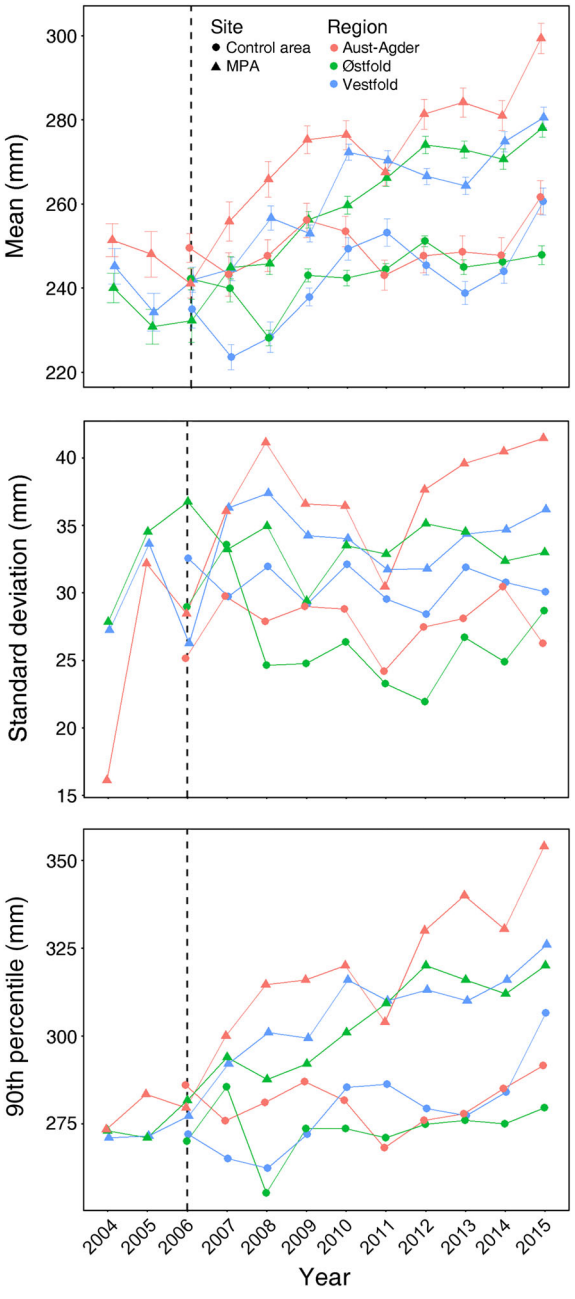

FIG. 6. Size-structure indicators of European lobster inside three MPAs and three control areas in southern Norway for the period 2004–2015.

management, environmental fluctuations, directional change, and extreme events. A greater range of sizes in MPAs, as shown here, provides an immediate buffering effect against environmental fluctuations (Planque et al. 2010), while any increases in population productivity and evolutionary changes, which might arise from the changes in size-dependent mortality documented here, can provide further buffering against both variability and directional change. In addition, if such longer-term ecological and evolutionary outcomes lead to larger population sizes, associated increases in genetic diversity (Pérez-Ruzafa et al. 2006, Pinsky and Palumbi 2014) can enhance adaptive capacity to climate change (Roberts et al. 2017).

In our study, the pattern of (1) high survival rates unaffected by body length at the MPAs and (2) low and length-dependent survival at the harvested areas was best supported in all regions up to 6 yr after protection. Such results emerged despite differences in geographic location (proximity to the open ocean vs. protected bay) and size of the protected areas, suggesting that immediate consequences of protection on lobster populations (i.e., rapid survival increase in all size classes) may not be influenced by such MPA features. However, the extended monitoring time revealed a somewhat diverging pattern during the late period (>6 yr after protection), with length effects in survival becoming best supported at two of the three MPAs while disappearing from the corresponding control areas. The fact that such changes occurred in the two smallest MPAs indicates that space limitations might influence survival patterns in the long term. On the other hand, late-period survival remained high for all size classes and indicators of size complexity were all significant only inside the largest marine MPA (Flødevigen), meaning that the size of the MPA relative to the home range of the species may play a fundamental role in the magnitude of the demographic and ecological responses after protection (Claudet et al. 2008). Indeed, home ranges of European lobster in Flødevigen marine MPA ranged between 5,728 and 41,548 m^2, which represents a mere 0.57–4.15% of the MPA area (1 km^2) (Moland et al. 2011*a*). A decreased home range: MPA area ratio would reduce the time the lobsters spend out of the MPA, therefore increasing their fitness and speeding up the expected demographic, ecological, and evolutionary effects (Villegas-Ríos et al. 2017).

Given that our models estimated apparent survival, mortality can be conflated with permanent emigration. Consequently, the later decreases in survival inside the no-take MPAs reported here may in fact reflect an increase in movement out of the MPA. Emigration can be a density-dependent response due to intensified territorial interactions among individuals in a limited space (Abesamis and Russ 2005), which are likely inside these lobster MPAs and especially the smallest ones. Indeed, high emigration rates have been documented for Atlantic cod in Flødevigen following increases in individual density several years after protection (Fernández-Chacón et al. 2015), and there are indications (i.e., catch per unit effort estimates) that lobster abundance levels have also increased in the studied MPAs (Moland et al. 2013). Recently, Thorbjørnsen et al. (2018) reported some spillover of large individuals off MPA boundaries in our study system but also some movement from harvested to protected areas (spill-in), especially in the Vestfold sites due to the proximity and existence of habitat corridors

between the local MPA and adjacent control area. In this sense, harvest of large individuals leaving the MPA and temporary use of the MPA by individuals from control areas (resulting in lower mortality risks) may explain part of the size-dependent survival patterns observed in later years at some MPA-Control area pairs. However, we are cautious with this explanation, as observed movements between MPAs and control areas are sparse (15 and 33 individuals leaving and entering MPAs, respectively; Thorbjørnsen et al. 2018), and other still unidentified causes may explain the survival increases seen outside our study MPAs.

We document that MPAs are a viable management approach for protecting against fisheries-induced selection, through the spatial refuge in both size-dependent and overall mortality. The extent that MPAs can help protect against fisheries-induced *evolution* (e.g., evolution of earlier maturation and growth rates; Hutchings and Fraser 2008, Swain 2011) will depend on the extent that the MPA system protects individuals with genotypes for relevant traits such as delayed maturation (Trexler and Travis 2000, Baskett et al. 2005, Miethe et al. 2010). In addition, such a response depends on connectivity between MPAs and harvested areas, with lower connectivity leading to greater evolutionary responses within MPAs, and greater connectivity leading to an averaging of selection across locations and therefore less protection within MPAs but more spillover from MPAs to areas outside (Baskett et al. 2005, Miethe et al. 2010). In a recent study, Sørdalen et al. (2018) used genetic parentage assignment to compare mating success in male European lobster in protected and harvested states. Their work clearly demonstrated a positive size-assortative mating pattern, where females have a strong disposition to mate with comparatively larger males, only realized in the protected population where large males were available as mates. Such assortative mating could act analogously to reduced connectivity in accentuating evolutionary responses within MPAs.

The vital rates measured here can inform about the expected rate and direction of ecological and evolutionary responses to MPAs. Such expectations, based on models parameterized with empirical data from natural populations, are crucial to an adaptive management process in the sense of Walters and Holling (1990), where a comparison of model projections to data can reveal whether MPAs are working as expected, and if not, what the drivers of such differences might be, and therefore whether changes in management might be necessary (White et al. 2011, 2013). Many models of anticipated ecological and evolutionary responses to MPAs (e.g., Baskett et al. 2005, White et al. 2013) assume constant mortality across sizes and ages in the absence of detailed data. Therefore, in addition to demonstrating the capacity for size-dependent mortality to work as an early indicator of MPA efficacy, the finding here of the potential for size-dependent mortality within MPAs highlights the importance of a poorly known demographic process in developing appropriate expectations for evaluating whether MPAs are achieving ecological and evolutionary goals.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2108/full